EGG DISPERSION IN TWO SPECIES OF PRAYING MANTIDS (MANTODEA: MANTIDAE)

R. M. EISENBERG AND L. E. HURD

Ecology Program, School of Life Sciences, University of Delaware, Newark, Delaware 19716.

Abstract. – Tenodera sinensis (Saussure) and Mantis religiosa (Linnaeus) are univoltine generalist predators which produce eggs at the end of the growing season. Oothecae of both species exhibit a markedly contagious dispersion in old fields in northern Delaware. In view of the large number of eggs contained in each ootheca, the propensity for synchronous egg hatch for each species, and severe food limitation during emergence early in the spring, such clumping is surprising since it places newly-hatched nymphs at a greater risk of cannibalism and competition from their cohort than if they were more uniformly distributed in space. Possible explanations for such clumping are discussed.

Key Words: Mantodea, Mantidae, Tenodera sinensis, Mantis regligiosa, dispersion, predators

The praying mantids Tenodera sinensis (Saussure) and Mantis religiosa (Linnaeus) are generalist predators which commonly occur in old fields in northern Delaware. Both species produce oothecae which may contain several hundred eggs each, and although eggs of T. sinensis generally hatch before those of M. religiosa, there is considerable intraspecific synchrony (Hurd and Eisenberg 1988a). Egg hatch occurs early in the spring, when there is normally a shortage of suitable prey (Hurd and Eisenberg 1988b. Rathet and Hurd 1983). We have shown that early instar nymphs of T. sinensis show a strong tendency to disperse (Hurd and Eisenberg 1984). We also know that first stadia of both species will resort to cannibalism when alternative food is absent (Hurd and Eisenberg 1984, unpublished laboratory observations). Given the above information, it would seem reasonable to expect that for both of these species, oothecae should not be clumped. Females which deposit an egg mass close to another egg mass would seem to be placing their young at a disadvantage in terms of increasing the potential for both intraspecific competition and cannibalism (Hurd 1988). We therefore decided to determine the spatial dispersion of oothecae of these two species in local old fields.

MATERIALS AND METHODS

Three different old fields in the vicinity of the University of Delaware campus in Newark, Delaware, were used for the collection of data. One was a late successional goldenrod field (field #1); the other two were sites AG (field #2) and CHRY (field #3) referred to by Hurd and Eisenberg (1988a, b). All three had been examined for several years and were known to harbor persistent populations of mantids.

The portion of each field which constituted mantid habitat was staked out. Areas thereby delineated were searched for oothecae and the location of each was marked with a 1.0 m wooden dowel. After searching Table 1. Results of oothecae censuses and nearest neighbor analyses for three fields. Ts = *Tenodera sinensis*, Mr = Mantis religiosa. R = ratio of observed mean distance to nearest neighbor to expected mean distance to nearest neighbor. *P* values are based on values of C (Clark and Evans 1954).

Site	Site Area (m ²)	Species	Number of Oothe- cae	R	P Value
Field #1	1200	Ts	119	0.76	<.01
Field #2	700	Ts	59	0.48	<.01
Field #3	1000	Мг	101	0.76	<.01

was completed the distance of each ootheca to two reference stakes was measured to the nearest cm using a pair of measuring tapes. In the laboratory this information was used to locate each ootheca on a scale map of each area, and dispersion was determined by nearest neighbor measurements (Clark and Evans 1954).

RESULTS AND DISCUSSION

While we encountered both species of mantids in each of our collections, only a single species was numerous enough in each field to permit dispersion analysis. In fields #1 and #2 the dominant mantid was T. sinensis, and oothecae were mainly located on dead, upright plant stems from 0.3 to 1.0 m above the ground. In field #3 the dominant mantid was M. religiosa, the oothecae of which were mainly found in the dense, overlapping grasses which comprised ground cover in these fields. In all three fields the nearest neighbor analysis shows a highly significant departure from random expectation (Table 1). An R value of 1.0 is expected if the observed pattern is random. Our R values of 0.48 to 0.76 indicate that the distributions of oothecae of both M. religiosa and T. sinensis are very contagious; both of these mantid species show a strong tendency to deposit egg masses in close proximity to other conspecific oothecae.

The average field-collected ootheca of T. sinensis weighs approximately 1.9 g and releases 240 nymphs (Eisenberg and Hurd

1977). Mean weight of *M. religiosa* oothecae collected from our study fields was 1.07 g, emergence ranging from 30 to 370 nymphs with a mean of 156. Both species display considerable synchrony of emergence in the field. Thus, in addition to the high local density produced by the hatching of a single ootheca, the close proximity of additional oothecae can result in even higher densities. In field #1, 29.4% of oothecae were within the same $1 m^2$ area as another ootheca and 48.7% were within the same 2 m² area. In field #2, 61.0% of oothecae were within the same 1 m² area as another ootheca and 71.2% were within the same 2 m² area. For field #3 the values were 19.8% and 30.7% respectively. Thus at emergence time, local densities of nymphs easily could reach or exceed 300 to 400 nymphs per m².

How can we explain the contagious nature of the oothecae pattern? During the late summer and fall of each year, T. sinensis often can be found on inflorescences of lateflowering plants such as goldenrods and asters, which attract prey in the form of flower-foraging insects including pollinators. This represents an important source of nutrition for females while they are undergoing oogenesis; females so positioned produce more eggs than those which are on plants not in flower (Hurd 1989). Females generally do not move around once they mature (Bartley 1982), so that a female's position on a specific plant (in flower or not) may be a matter of chance rather than choice. However, the clonal nature of these flowering plants produces clumps of the most nutritionally rewarding oviposition sites, which could in turn explain contagion among oothecae. An alternative explanation, that females oviposit more than once, is less likely because normally there is not sufficient time between first oviposition and killing frost for this species to generate a second ootheca in our geographical region in the face of rapidly decreasing food levels at the end of the growing season (Eisenberg, Hurd and Bartlev 1981).

Mantis religiosa exhibits a very different set of behaviors in regard to its foraging activities. This species tends to forage closer to the ground than T. sinensis (Rathet and Hurd 1983), and thus is less likely to be found on the taller flowering plants. While this species also will deposit its oothecae on upright stems, apparently it prefers grasses located much closer to the ground. These grasses do not have flowers to attract supplemental food, and constitute a much denser, less patchy vegetational layer than goldenrod. We do not know if this species faces the same degree of food limitation as T. sinensis at the end of the growing season, so that it is possible that multiple oviposition is responsible for the contagious distribution of M. religiosa oothecae. However, this still leaves open the question as to why a female would crowd her own offspring, an apparently maladaptive trait.

Acknowledgments

This work was supported by NSF grant BSR 8506181. This is contribution #137 from the Ecology Program, University of Delaware.

LITERATURE CITED

Bartley, J. A. 1982. Movement patterns of adult male and female mantids (*Tenodera stnensis* Saussure). Environmental Entomology 11: 1108–1111.

Clark, P. J. and F. C. Evans. 1954. Distance to nearest

neighbor as a measure of spatial relationships in populations. Ecology 35: 445–453.

- Eisenberg, R. M. and L. E. Hurd. 1977. An ecological study of the emergence characteristics for egg cases of the Chinese mantis (*Tenodera aridifolia sinensis* Saussure). American Midland Naturalist 97: 478– 482.
- Eisenberg, R. M., L. E. Hurd, and J. A. Bartley. 1981. Ecological consequences of food limitation for adult mantids *Tenodera sinensis* Saussure). American Midland Nat. 106: 209–218.
- Hurd, L. E. 1988. Consequences of divergent egg phenology to predation and coexistence in two sympatric, congeneric mantids (Orthoptera: Mantidae). Oecologia 76: 547–550.
- . 1989. The importance of late season flowers to the fitness of an insect predator, *Tenodera sinensis* Saussure (Orthoptera: Mantidae), in an old field community. Entomologist (U.K.) 108: 223– 228.
- Hurd, L. E. and R. M. Eisenberg. 1984. Experimental density manipulations of the predator *Tenodera* sinensis (Orthoptera: Mantidae) in an old-field community. 1. Mortality, development and dispersal of juvenile mantids. Journal Animal Ecology 53: 269–281.
- 1988b. Temporal distribution of hatching times in three sympatric mantids (Mantodea: Mantidae) with implications for niche separation and coexistence. Proceedings Entomological Society Washington 91: 55–58.
- Rathet, I. H. and L. E. Hurd. 1983. Ecological relationships among three co-occurring mantids. *Tenodera sinensis* (Saussure), *T. angustipennis* (S.), and *Mantis religiosa*. American Midland Naturalist 110: 240–248.